Extinction in Discrete, Competitive, Multi-species Patch Models

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Abstract

In this paper we extend the results of Franke and Yakubu in [5] for extinction in discrete competitive patch models. For a system of n species on m patches, we define conditions under which one species is a "superior competitor" to another and show that this is sufficient for one species to drive another to extinction. We also illustrate the result with an example for three species on three patches.

1 Introduction

Dispersal between patches has been shown to play a significant role in the dynamics of populations that are distributed over multiple habitats or patches, often stabilizing complex dynamics [1, 7, 9]. Hastings [6] showed that passive dispersal will never be selected for in a temporally constant environment, even if there is spatial variation among patches. However, dispersal may be advantageous in a temporally varying environment [8].

Franke and Yakubu analyzed discrete-time competitive systems in [2, 3], including dispersal of one species in [4]. In [5], Franke and Yakubu explored a discrete competitive system of n species dispersing between 2 patches. They found conditions under which one species could drive another to extinction. Here we extend their results to n species on m patches and provide an example showing the importance of dispersal to the dynamics of the model.

2 Preliminaries

Consider the following system,

$$(\mathbf{x_1}(t+1), \mathbf{x_2}(t+1), \ldots, \mathbf{x_m}(t+1)) = F(\mathbf{x_1}(t), \mathbf{x_2}(t), \ldots, \mathbf{x_m}(t)), \tag{1}$$

for n species on m patches which takes the form of $n \cdot m$ equations. For each $1 \leq i \leq m$, $1 \leq j \leq n$, and $(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in \Re_+^n \times \Re_+^n \times \cdots \times \Re_+^n$ (m-times) where $\mathbf{x_i} = (x_{i,1}, x_{i,2}, \ldots, x_{i,n})$ we define $x_{i,j}(t+1) = F_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})$ where $F_{i,j} : \Re_+^n \times \Re_+^n \times \cdots \times \Re_+^n \to \Re_+$. In particular $F_{i,j}$ takes the form

$$\begin{aligned} F_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) &= x_{i,j}(t) g_{i,j}\left(\sum_{k=1}^{n} \alpha_{i,j,k} x_{i,k}(t)\right) \\ &- \delta_j \left[x_{i,j}(t) g_{i,j}\left(\sum_{k=1}^{n} \alpha_{i,j,k} x_{i,k}(t)\right)\right. \\ &- \left. \frac{1}{m} \sum_{h=1}^{m} x_{h,j}(t) g_{h,j}\left(\sum_{k=1}^{n} \alpha_{h,j,k} x_{h,k}(t)\right)\right] \end{aligned}$$

where $x_{i,j}(t)$ is species j in patch i at generation t, $g_{i,j} : \Re_+^n \to \Re_+$ are monotone decreasing functions, $\alpha_{i,j,k}$ is the competition coefficient in patch i for species k with respect to species j, and $\delta_j \in [0,1]$ measures the diffusion of species j between the patches. $\delta_j = 0$ corresponds to no diffusion and when $\delta_j = 1$, species j disperses so population sizes are equal across all patches. We define F^t as the map F composed with itself t times.

Consider for species j, $\delta_j = 0$ where there is no diffusion between patches. This would simplify $F_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) = F_{i,j}(\mathbf{x_i}) = x_{i,j} g_{i,j}(\mathbf{x_i})$. Further if we assume that there were no other species on patch i then we have $F_{i,j}(x_{i,j}) = x_{i,j} g_{i,j}(x_{i,j})$. This is a one-dimensional map. Let x^* be the unique positive fixed point for this map which exists by assumption. If $0 < x < x^*$, then $F_{i,j}(x) > x$. If $x > x^*$, then $F_{i,j}(x) < x$. So under iteration of $F_{i,j}$, $I_{i,j} = F_{i,j}([0, x^*])$ is the largest attracting invariant interval in $\Re_+$. The following shows that based on these competitive assumptions on the $g_{i,j}$ the populations will not grow without bound.

Lemma 1: In system (2), no point has an unbounded orbit.

Proof: Let $(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in \Re_+^n \times \Re_+^n \times \cdots \times \Re_+^n$. To show that orbits are bounded we need to show that the sequences $\left\{F_{i,j}^t(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})\right\}_{t \geq o}$ are bounded. To do this we first show that for each species j,

$$\max_i \{F_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \leq \max_i \left\{ x_{i,j}(t) g_{i,j}\left(\sum_{k=1}^{n} \alpha_{i,j,k} x_{i,k}(t)\right)\right\}.$$

By definition

$$\begin{aligned}F_{i,j}(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) &= x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right)\\ &- \delta\left[x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right)\right.\\ &- \left.\frac{1}{m}\sum_{h=1}^{l}x_{h,j}(t)g_{h,j}\left(\sum_{k=1}^{n}\alpha_{h,j,k}x_{h,k}(t)\right)\right].\end{aligned}$$

If

$$x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right) \geq \max_{\beta\neq i} x_{\beta,j}(t)g_{\beta,j}\left(\sum_{k=1}^{n}\alpha_{\beta,j,k}x_{\beta,k}(t)\right),$$

then

$$\begin{aligned}F_{i,j}(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) &\leq x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right)\\ &= \max_i\left\{x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right)\right\}.\end{aligned}$$

If

$$x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right) \leq \max_{\beta\neq i} x_{\beta,j}(t)g_{\beta,j}\left(\sum_{k=1}^{n}\alpha_{\beta,j,k}x_{\beta,k}(t)\right),$$

then

$$\begin{aligned}F_{i,j}(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) &\leq \max_{\beta\neq i} x_{\beta,j}(t)g_{\beta,j}\left(\sum_{k=1}^{n}\alpha_{\beta,j,k}x_{\beta,k}(t)\right)\\ &= \max_i\left\{x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right)\right\}.\end{aligned}$$

Thus $\max_i\{F_{i,j}(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m})\} \leq \max_i\{x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right)\}$.

Further because each $g_{i,j}$ is monotone decreasing

$$x_{i,j}(t)g_{i,j}\left(\sum_{k=1}^{n}\alpha_{i,j,k}x_{i,k}(t)\right) \leq x_{i,j}(t)g_{i,j}\left(x_{i,j}(t)\right)$$

with $\alpha_{i,j,j} = 1$. Recall that if $x_{i,j} < \max I_{i,j}$, then $F_{i,j}(x_{i,j}) \leq \max I_{i,j}$. Also if $x_{i,j} > \max I_{i,j}$, then $F_{i,j}(x_{i,j}) < x_{i,j}$. Thus for each $1 \leq i \leq m$, $1 \leq j \leq n$, and each point $(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) \in \Re_+^n \times \Re_+^n \times \cdots \times \Re_+^n$ we have $\max\{F_{i,j}\} \leq$

$\max_{i,j}\{x_{i,j}, \max I_{i,j}\}$. Therefore the sequences $\left\{F^t_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})\right\}_{t\geq o}$ are bounded for $1 \leq i \leq m$ and $1 \leq j \leq n$. This completes the proof.

Additionally we have the following:

Lemma 2: In system (1), the $\omega-$limit set of every point in $\Re^n_+ \times \Re^n_+ \times \cdots \times \Re^n_+$ is a nonempty subset of the compact invariant set $B \cap W$, where $B = \left\{(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in \Re^n_+ \times \Re^n_+ \times \cdots \times \Re^n_+ \middle| \text{ for each } 1 \leq j \leq n, \max_j\{x_{i,j}\} \leq \max_i\{\max I_{i,j}\}\right\}$, and $W = \left\{(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in \Re^n_+ \times \Re^n_+ \times \cdots \times \Re^n_+ \middle| \text{ for each } 1 \leq i, k \leq m \text{ and } 1 \leq j \leq n, \frac{\delta_j}{m-(m-1)\delta_j} x_{i,j}(t+1) \leq x_{k,j}(t+1) \leq \frac{m-(m-1)\delta_j}{\delta_j} x_{i,j}(t+1)\right\}$.

Proof: Let $(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in \Re^n_+ \times \Re^n_+ \times \cdots \times \Re^n_+$ then from Lemma 1 we have that $\omega(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in \Re^n_+ \in B$. To show that $\omega(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in W$, we observe the following where $\delta_j \in (0,1)$. For convenience we will write $g_{i,j}\left(\sum_{k=1}^n \alpha_{i,j,k} x_{i,k}(t)\right)$ as $g_{i,j}(\cdot)$. Without loss of generality consider species j on patch 1 we have

$$\begin{aligned} F_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) &= \left(1 - \frac{m-1}{m}\delta_j\right) x_{1,j}(t) g_{1,j}(\cdot) \\ &+ \frac{\delta_j}{m} x_{2,j}(t) g_{2,j}(\cdot) + \cdots + \frac{\delta_j}{m} x_{m,j}(t) g_{m,j}(\cdot) \end{aligned}$$

Next multiplying by $\frac{m-(m-1)\delta_j}{\delta_j}$ yields

$$\begin{aligned} \frac{m-(m-1)\delta_j}{\delta_j} F_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) &= \frac{(m-(m-1)\delta_j)^2}{\delta_j m} x_{1,j}(t) g_{1,j}(\cdot) \\ &+ \frac{m-(m-1)\delta_j}{\delta_j} \frac{\delta_j}{m} x_{2,j}(t) g_{2,j}(\cdot) + \cdots \\ &+ \cdots + \frac{m-(m-1)\delta_j}{\delta_j} \frac{\delta_j}{m} x_{m,j}(t) g_{m,j}(\cdot) \end{aligned}$$

Since $\frac{m-(m-1)\delta_j}{\delta_j} \geq 1$ we have $\frac{m-(m-1)\delta_j}{\delta_j}\frac{\delta_j}{m} \geq \frac{\delta_j}{m}$ and $\frac{m-(m-1)\delta_j}{\delta_j}\left(1 - \frac{m-1}{m}\delta_j\right) = \frac{(m-(m-1)\delta_j)^2}{\delta_j m} \geq \left(1 - \frac{m-1}{m}\delta_j\right)$. So comparing term by term with $F_{k,j}$, we have that $F_{k,j} \leq \frac{m-(m-1)\delta_j}{\delta_j} F_{i,j}$ as well as $F_{k,j} \geq \frac{\delta_j}{m-(m-1)\delta_j} F_{i,j}$ thus

$$\frac{\delta_j}{m-(m-1)\delta_j} F_{i,j} \leq F_{k,j} \leq \frac{m-(m-1)\delta_j}{\delta_j} F_{i,j}.$$

Finally since $x_{i,j}(t+1) = F_{i,j}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})$ we obtain

$$\frac{\delta_j}{m-(m-1)\delta_j} x_{i,j} \leq x_{k,j} \leq \frac{m-(m-1)\delta_j}{\delta_j} x_{i,j}.$$

This completes the proof.

3 Results

For this model we assume that each species will diffuse between the m patches at a particular rate, given by the δ_k's. For species k, if the rate $\delta_k = 0$ then there is no diffusion, where if $\delta_k = 1$ then the populations will diffuse so that the populations in each patch will be equal. We show that in this model a species can drive another species to extinction if particular conditions are met. We define these conditions here.

For system (1) and $\delta_k, \delta_n \in (0, 1]$, a species k is superior to species n if on some patch i and for some constant $c > 0$ for all points $(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in B \cap W$, we have

$$\begin{aligned} (i) \quad & (1-\delta_n) g_{i,n}(\cdot) + \frac{\delta_n}{m}\left(\frac{m-(m-1)\delta_n}{\delta_n}\right)\sum_{h=1}^{m} g_{h,n}(\cdot) \\ < \quad & \left((1-\delta_k) g_{i,k}(\cdot) + \frac{\delta_k}{m}\left(\frac{\delta_k}{m-(m-1)\delta_k}\right)\sum_{h=1}^{m} g_{h,k}(\cdot)\right)^{c} \end{aligned}$$

or

$$\begin{aligned} (ii) \quad & \frac{m-(m-1)\delta_n}{m}\left(g_{i,n}(\cdot) + \left(\frac{m-(m-1)\delta_n}{\delta_n}\right)\sum_{l=1, l\neq i}^{m} g_{l,n}(\cdot)\right) \\ < \quad & \left(\left(\frac{\delta_k}{\delta_k + (m-1)(m-(m-1)\delta_k)}\right)\left(g_{i,k}(\cdot)\right.\right. \\ + \quad & \left.\left.\left(\frac{\delta_k}{m-(m-1)\delta_k}\right)\sum_{l=1, l\neq i}^{m} g_{l,k}(\cdot)\right)\right)^{c} \end{aligned}$$

We note here that these conditions depend on the linear combination of the growth rates and well as the diffusion rates. Also note that for a diffusion rate of 1 these conditions simplify to having the average growth rate of the species k being larger that the average growth rate of species n.

Theorem 1: For system (1), if species k is superior to species n, then species n will go extinct.

Proof: Note that by Lemma 2 we have that the $\omega-$limit set of every point is a nonempty subset of the compact invariant set $B \cap W$. Let $(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \in B \cap W$. We will show that $F_{i,n}^{t_i}(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) \to 0$ as $t_i \to \infty$ for $1 \leq i \leq m$.

Suppose inequality (i) is satisfied on patch i so species k is superior to species n. Consider the function $V : \Re_+^n \times \Re_+^n \times \cdots \times \Re_+^n \to \Re_+$ where $V(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) = \frac{x_{i,n}}{x_{i,k}^c}$. We show that V decreases along the orbit so that $x_{l,n} = 0$ for $1 \leq l \leq m$, thus V is a Lyapunov function.

Let $x_{l,k}, x_{l,n} > 0$ for $1 \leq l \leq m$, then we have

$$\frac{V(F(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}))}{V(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})} = \frac{(1-\delta_n)x_{i,n}(t)g_{i,n}\left(\cdot\right) + \frac{\delta_n}{m}\sum_{h=1}^{m} x_{h,n}(t)g_{h,n}\left(\cdot\right)}{\left((1-\delta_k)x_{i,k}(t)g_{i,k}\left(\cdot\right) + \frac{\delta_k}{m}\sum_{h=1}^{m} x_{h,k}(t)g_{h,k}\left(\cdot\right)\right)^c} \frac{x_{i,k}^c}{x_{i,n}}$$

Using the inequality $\frac{\delta_j}{m-(m-1)\delta_j} x_{i,j}(t+1) \leq x_{h,j}(t+1) \leq \frac{m-(m-1)\delta_j}{\delta_j} x_{i,j}(t+1)$ we get

$$\begin{aligned}
& \frac{V(F(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}))}{V(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})} \\
\leq \quad & \frac{(1-\delta_n)x_{i,n}(t)g_{i,n}\left(\cdot\right) + \frac{\delta_n}{m}\left(\frac{m-(m-1)\delta_n}{\delta_n}\right)\sum_{h=1}^{m} x_{i,n}(t)g_{h,n}\left(\cdot\right)}{\left((1-\delta_k)x_{i,k}(t)g_{i,k}\left(\cdot\right) + \frac{\delta_k}{m}\left(\frac{\delta_k}{m-(m-1)\delta_k}\right)\sum_{h=1}^{m} x_{i,k}(t)g_{h,k}\left(\cdot\right)\right)^c} \frac{x_{i,k}^c}{x_{i,n}} \\
= \quad & \frac{(1-\delta_n)g_{i,n}\left(\cdot\right) + \frac{\delta_n}{m}\left(\frac{m-(m-1)\delta_n}{\delta_n}\right)\sum_{h=1}^{m} g_{h,n}\left(\cdot\right)}{\left((1-\delta_k)g_{i,k}\left(\cdot\right) + \frac{\delta_k}{m}\left(\frac{\delta_k}{m-(m-1)\delta_k}\right)\sum_{h=1}^{m} g_{h,k}\left(\cdot\right)\right)^c}.
\end{aligned}$$

So from inequality (i) we have that $\dfrac{V(F(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}))}{V(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})} < 1$.

On the other hand, suppose inequality (ii) is satisfied on patch i so species k is superior to species n. Consider the function $V : \Re_+^n \times \Re_+^n \times \cdots \times \Re_+^n \to \Re_+$ where $V(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m}) = \dfrac{\sum_{l=1}^{m} x_{l,n}}{\left(\sum_{l=1}^{m} x_{l,k}\right)^c}$. Let $x_{l,k}, x_{l,n} > 0$ for $1 \leq l \leq m$, we have

$$\frac{V(F(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})}{V(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})} = \frac{\sum_{l=1}^{m} x_{l,n}(t)g_{l,n}\left(\cdot\right)}{\left(\sum_{l=1}^{m} x_{l,k}(t)g_{l,k}\left(\cdot\right)\right)^c} \frac{\left(\sum_{l=1}^{m} x_{l,k}\right)^c}{\sum_{l=1}^{m} x_{l,n}}$$

Again using the inequality $\frac{\delta_j}{m-(m-1)\delta_j} x_{h,j}(t+1) \leq x_{l,j}(t+1) \leq \frac{m-(m-1)\delta_j}{\delta_j} x_{i,j}(t+1)$ we get

$$\begin{aligned}
\frac{V(F(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})}{V(\mathbf{x_1}, \mathbf{x_2}, \ldots, \mathbf{x_m})} \quad \leq \quad & \frac{x_{i,n}g_{i,n}(\cdot) + \left(\frac{m-(m-1)\delta_n}{\delta_n}\right)\sum_{l=1, l\neq i}^{m} x_{i,n}(t)g_{l,n}\left(\cdot\right)}{\left(x_{i,k}g_{i,k}(\cdot) + \left(\frac{\delta_k}{m-(m-1)\delta_k}\right)\sum_{l=1, l\neq i}^{m} x_{i,k}(t)g_{l,k}\left(\cdot\right)\right)^c} \\
\cdot \quad & \frac{\left(x_{i,k} + (m-1)\left(\frac{m-(m-1)\delta_k}{\delta_k}\right)x_{i,k}\right)^c}{x_{i,n} + (m-1)\left(\frac{\delta_n}{m-(m-1)\delta_n}\right)x_{i,n}} \\
= \quad & \frac{g_{i,n}(\cdot) + \left(\frac{m-(m-1)\delta_n}{\delta_n}\right)\sum_{l=1, l\neq i}^{m} g_{l,n}\left(\cdot\right)}{\left(g_{i,k}(\cdot) + \left(\frac{\delta_k}{m-(m-1)\delta_k}\right)\sum_{l=1, l\neq i}^{m} g_{l,k}\left(\cdot\right)\right)^c} \\
\cdot \quad & \frac{\left(\frac{\delta_k + (m-1)(m-(m-1)\delta_k)}{\delta_k}\right)^c}{\frac{m}{m-(m-1)\delta_n}}
\end{aligned}$$

From inequality (ii) we have that $\dfrac{V(F(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}))}{V(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m})} < 1$. Thus from either inequality we obtain that V is a decreasing along orbits for $(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) \in B \cap W$ with $x_{l,k}, x_{l,n} > 0$ for $1 \le l \le m$. Let $(\mathbf{p_1},\mathbf{p_2},\ldots,\mathbf{p_m}) \in \omega(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m})$, then by definition there exist a sequence $t_i \to \infty$ where $F^{t_i}(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) \to ((\mathbf{p_1},\mathbf{p_2},\ldots,\mathbf{p_m})$. We want to show that $F^{t_i}_{l,n}(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) \to 0$ as $t_i \to \infty$.

If $p_{i,k}, p_{i,n} > 0$ then we have that $\dfrac{V(F(\mathbf{p_1},\mathbf{p_2},\ldots,\mathbf{p_m}))}{V(\mathbf{p_1},\mathbf{p_2},\ldots,\mathbf{p_m})} < 1$. This cannot hold for an $\omega-$limit point, which implies that $p_{i,n} = 0$ and $p_{i,k} > 0$. If $p_{i,n} > 0$ and $p_{i,k} = 0$ then the sequence $\{F^{t_i}(\mathbf{p_1},\mathbf{p_2},\ldots,\mathbf{p_m})\}$ would be unbounded which is a contradiction. From Lemma 2 we conclude that if $p_{i,n} = 0$ then $p_{l,n} = 0$ for $1 \le l \le m$. Thus $\omega(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) \subset \{(\mathbf{x_1},\mathbf{x_2},\ldots,\mathbf{x_m}) \in \Re^n_+ \times \Re^n_+ \times \cdots \times \Re^n_+ | x_{l,n} = 0, 1 \le l \le m\}$.

Finally, consider the points that do not enter $B \cap W$ on which species k is superior to species n. Since each condition is a strict inequality we have that these hold on a neighborhood of $B \cap W$. From Lemma 1, we have that every point must enter this neighborhood that on every orbit, V is eventually decreasing and the result holds for every point with $x_{l,k}, x_{l,n} > 0$. This completes the proof.

4 Example

In this section we illustrate the importance of dispersal with a three-species, three-patch example. We take $g_{i,j} = \exp\left(r_{i,j} - \sum_{k=1}^{3} \alpha_{i,j,k} x_{i,k}\right)$ with $r_{11} = 1.5$, $r_{22} = 1.4$, $r_{33} = 1.3$, and all other $r_{i,j} = 1.1$, $i \neq j$, and all $\alpha_{i,j} = 0.1$. If there is complete dispersal, so $\delta_1 = \delta_2 = \delta_3 = 1$, then the average growth rate of species 1 is the highest and it is a superior competitor to both species 2 and species 3, driving them to extinction by Theorem 1 (with $c = 1$).

When there is no dispersal, so $\delta_1 = \delta_2 = \delta_3 = 0$, a different species persists in each patch (species 1 in patch 1, species 2 in patch 2, and species 3 in patch 3) driving all other species to extinction. If we set $\delta_1 = \delta_2 = \delta_3 = \delta$, then as δ increases from 0 to 1 we see coexistence for low δ, see Figure 1. Increasing further we observe species 3 becomes extinct and species 1 and 2 coexist on each patch. For δ closer to 1 only species 1 persists on all three patches. It is clear through this example that dispersal has strong influence on the dynamics of the entire system.

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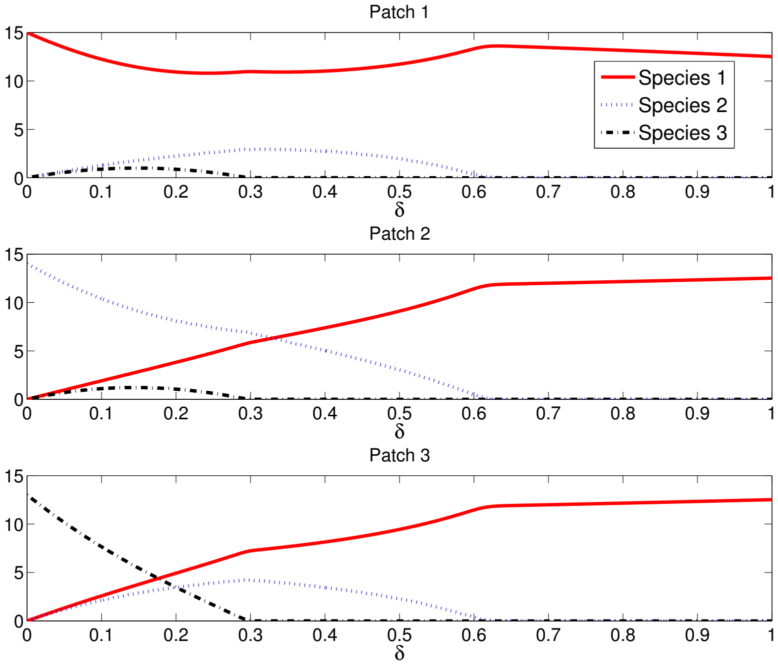

Figure 1: Model (1) with $g_{i,j} = \exp\left(r_{i,j} - \sum_{k=1}^{3} \alpha_{i,j,k} x_{i,k}\right)$ where $r_{11} = 1.5$, $r_{22} = 1.4$, $r_{33} = 1.3$, $r_{i,j} = 1.1$, $i \neq j$, and all $\alpha_{i,j} = 0.1$ All species disperse at the same rate ($\delta_1 = \delta_2 = \delta_3 = \delta$). Equilibrium values for each species plotted against δ.

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